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MEHIS ROHTLA

Otolith sclerochronological studies on migrations, spawning habitat preferences and age of freshwater fishes inhabiting the Baltic Sea

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Estonian Marine Institute and Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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"Fishes do not thrive in cold places, and those fishes suffer most in severe winters that have a stone in their head…; for owing to the stone they get frozen with the cold, and are thrown up on shore."
Probably the first scientific observation about otoliths, in Aristotle's "History of Animals".

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Rohtla, M., Vetemaa, M., Urtson, K. & Soesoo, A. 2012. Early life migration patterns of Baltic Sea pike *Esox lucius*. *Journal of Fish Biology* 80, 886–893.

II Rohtla, M., Vetemaa, M., Taal, I., Svirgsden, R., Urtson, K., Saks, L., Verliin, A., Kesler, M. & Saat, T. 2014. Life history of anadromous burbot (*Lota lota*, Linneaus) in the brackish Baltic Sea inferred from otolith microchemistry. *Ecology of Freshwater Fish* 23, 141–148.

III Rohtla, M., Vetemaa, M., Svirgsden, R., Taal, I., Saks, L., Kesler, M., Verliin, A. & Saat, T. 2014. Using otolith $^{87}Sr:^{86}Sr$ as a natal chemical tag in the progeny of anadromous Baltic Sea pike (*Esox lucius*) – a pilot study. *Boreal Environment Research* 19, 379–386.

IV Rohtla, M., Taal, I., Svirgsden, R. & Vetemaa, M. 2015. Old timers from the Baltic Sea: revisiting the population structure and maximum recorded age of ide *Leuciscus idus*. *Fisheries Research* 165, 74–78.

V Rohtla, M., Svirgsden, R., Taal, I., Saks, L., Eschbaum, R. & Vetemaa, M. 2015. Life history characteristics of ide *Leuciscus idus* in the Eastern Baltic Sea. *Fisheries Management and Ecology* (in press.).

VI Rohtla, M. & Vetemaa, M. Prevalence of freshwater spawning amongst pike (*Esox lucius*) in the Väinameri Sea, Baltic Sea. Manuscript.

The author contributed substantially to all the papers, generated the original ideas, took active part in data collection, was responsible for chemical and data analysis, and was the leading author of all six publications.

1. INTRODUCTION

The fish fauna of the Baltic Sea comprises a mixture of marine and freshwater species. Fish species richness is low and there are no endemic species because the Baltic Sea is young on a geological time scale (i.e. 7000–10000 years old) (Voipio 1981; Ojaveer & Pihu 2003). As the Baltic Sea has been, is and will be relatively dynamic in terms of salinity, temperature and oxygen regimes (Voipio 1981; Meier et al. 2012), it is not an ideal habitat for fully marine or freshwater species, with many living at their physiological limits (Ojaveer & Pihu 2003). Nevertheless, several marine and freshwater species have adapted to the low salinities of the Baltic Sea and in some cases subspecies have formed (e.g. Baltic herring *Clupea harengus membras*, Baltic cod *Gadus morhua callarias*) (Ojaveer et al. 2003). These fishes thrive on the nutrient rich waters of the Baltic Sea and complete an extremely productive food chain. However, many regions are also negatively affected by eutrophication (e.g. algal blooms, oxygen deprivation) resulting mainly from anthropogenic nutrient pollution (HELCOM 2010; Voss et al. 2011). In addition, the effects of overfishing, climatic fluctuations and habitat destruction/degradation are pronounced in the Baltic Sea and its freshwater basins (Möllmann et al. 2008; Eriksson et al. 2009; Sundblad & Bergström 2014; Nilsson et al. 2014). All of these factors interact and have produced cascading ecosystem effects that can eventually lead to regime shifts in food chains where top-down control is weakened and bottom-up control prevails (Möllmann et al. 2008; Ljunggren et al. 2010).

While truly marine fishes make up the vast majority of fish biomass and catches in the Baltic Sea, species of freshwater origin are also ecologically and economically important (Ojaveer et al. 2003). The latter can be fully dependent on freshwater spawning (e.g. vimba bream *Vimba vimba* (Erm et al. 2003a)), partly dependent on freshwater spawning (e.g. pike *Esox lucius* (Engstedt et al. 2010)) or not dependent on freshwater spawning (e.g. pike-perch *Sander lucioperca* (Erm et al. 2003b)). The present thesis focuses on the freshwater origin species that are fully or partly dependent on freshwater spawning. Brackish water living species that depend on freshwater spawning are generally referred to as anadromous or semi-anadromous (Müller & Berg 1982; Ojaveer et al. 2003; Koporikov & Bogdanov 2011). Compared to marine waters, reproduction in fresh water has several advantages: (1) more favourable environmental conditions (e.g. salinity, temperature) for spawning and successful development of eggs and larvae; (2) rich food resource for larvae and juveniles; (3) generally low predation pressures. Although different freshwater-running Baltic Sea fishes form an important part of commercial and recreational fisheries, large knowledge gaps still exist in their biology (excluding the salmonids) – information which is crucial for sustainable stock management. Not much is known about the prevalence and spatial variation of anadromous behaviour, migration patterns, recruitment and connectivity. For example, shifts in spawning habitat may indicate alterations in the quality and accessibility of

spawning grounds. For most species, there is also a lack of standard age and growth rate data.

Anadromous fish are regarded as one of the most threatened vertebrate groups in the world and they present special conservation challenges (Jonsson et al. 1999; Miles et al. 2014). Completion of their life cycle does not only depend on the ecological quality of fresh- and seawater habitats, but also on the accessibility of spawning areas. Negative effects from anthropogenic activities such as damming, habitat destruction/degradation/alternation, pollution and the introduction of alien species or diseases, are more pronounced in freshwaters owing to the more limited amount of this habitat compared to marine waters. As a large amount of freshwater habitat has already been destroyed or is inaccessible to anadromous fishes, the focus needs to be shifted towards conserving those habitats still present and restoring the suitable habitats that are already destroyed. In order for conservation actions to be successful, the same basic information is needed about the biology of these species as is required by commercial fisheries. Again, knowledge on migration patterns, recruitment and connectivity are crucial. These issues can be tackled in several ways (Lucas & Baras 2001), but usually involve some kind of applied or natural tag.

One such method uses otoliths as natural chemical "tags" to provide information about individuals' life histories (Campana 1999; Walther & Limburg 2012). Otoliths are calcified structures located in the inner-ear of all teleost fishes; they help the fish to detect sound and gravity, and maintain balance (Popper et al. 2005). Otoliths are generally precipitated in the form of aragonite, but vateritic otoliths may occur (Tzeng et al. 2007). All fishes hold three pairs of otoliths, however the morphology of these pairs varies among species (Popper et al. 2005). The largest of the otoliths (usually sagitta) is most often used in fisheries science. Otoliths start to form early during embryogenesis and grow continuously throughout a fish's life (Riley et al. 1997). This growth can be followed and quantified using the daily or annual growth rings (Campana & Thorrold 2001). Deposition of daily increments follows a circadian rhythm and is generally observable only during the first six months of life, after which daily rings become compressed and are no longer visible (Campana & Neilson 1985). Annual growth rings are generated by extreme environmental events (e.g. winter, flooding) that result in suppressed or accelerated feeding (Campana & Thorrold 2001). Excellent chronological properties and lack of resorption make otoliths an ideal tool for age and growth studies (Campana & Thorrold 2001).

Otoliths also incorporate different chemical elements from the ambient environment. Calcium, carbon and oxygen are the major elements that make up the $CaCO_3$ matrix of otoliths. However, different minor and trace elements are also incorporated to otoliths (reviewed by Campana 1999). Notably, strontium arbitrarily substitutes for calcium because their ions are of similar size and share the same valence. So far, 50 elements have been quantified from otoliths (Campana 1999; Chen & Jones 2006). Most of these elements are unfortunately controlled by ionic regulation and therefore do not reflect the chemical

composition of the ambient environment (Campana 1999). Elements (e.g. Sr, Ba, Mg, Mn) and stable isotope ratios (^{87}Sr:^{86}Sr, $\delta^{13}C$, $\delta^{18}O$) not regulated within the fish and that can be accurately quantified are mostly used in fisheries science for making inferences about individual life histories (Campana 1999; Elsdon et al. 2008; Walther & Limburg 2012).

By coupling the time-recording and element-incorporating properties of otoliths, it is possible to retrospectively investigate various life history aspects that are otherwise difficult or impossible to address. These inferences are made without interfering in a fish's life (until the end, when the fish is sacrificed) and can be obtained relatively fast – important advantages compared to conventional telemetry and tagging methods. It is generally thought that fish otoliths reflect the chemical composition of the surrounding water and change in time according to fish movements and/or variations in ambient chemistry (Campana 1999; Walther & Limburg 2012). Therefore, if different waterbodies (or parts of them) have distinct chemical compositions and the specimens under study migrate between them, then these movements should be visible in the chemical profiles of their otoliths. For example, it is widely known that the Sr:Ca ratio is usually several times higher in sea water than in fresh water, which allows for reconstruction of fish movements between such waters (e.g. Secor & Rooker 2000; Walther & Limburg 2012). Reconstructing such migrations is the most widespread and universal application in the field of otolith microchemistry, including in the Baltic Sea (Westin & Limburg 2002; Shiao et al. 2006; Engstedt et al. 2010, 2012). However, freshwater Sr:Ca can be equal or even higher than that of the sea and therefore caution is warranted in systems with high Sr:Ca freshwater endmembers (Kraus & Secor 2004; Brown & Severin 2009). Similarly, the Ba:Ca ratio in fresh water is usually higher than in sea water and can also be used for inferring fish migration patterns (e.g. Elsdon & Gillanders 2005; Mohan et al. 2015), but varying degrees of success have been reported in its use (Crook et al. 2006; Hamer et al. 2006; Jessop et al. 2012; Smith & Kwak 2014). Although in some (tide-influenced) systems the Ba:Ca ratios outperform the Sr:Ca ratios as markers for migrations (Nims & Walther 2014; Mohan et al. 2015).

With the help of otolith Sr:Ca and/or Ba:Ca profiles, it is possible to determine whether an individual hatched in fresh water or at sea, and how it moved between these habitats (e.g. Kafemann et al. 2000; Shiao et al. 2006; Magath et al. 2013). For example, otolith Sr:Ca profiles have been used to demonstrate that European eel (*Anguilla anguilla*) are not, as was widely believed, an obligatorily catadromous species, but should be regarded as facultatively catadromous instead (Tsukamoto et al. 1998; Daverat et al. 2006). Such a discovery may have otherwise required years of tracking these animals with conventional methods (e.g. tagging, telemetry). Similarly, it is difficult to track the early life movements of fish with conventional methods simply because of a lack of artificial and natural markers that can track the fish from early ontogeny to adulthood. Addressing fish movement patterns with Sr:Ca and

Ba:Ca profiles has proven to be especially useful with diadromous species, as migrations across freshwater-seawater boundaries are generally well recorded in otoliths (e.g. Feutry et al. 2011; Miller et al. 2011). However, the visibility of these transitions on elemental profiles depends on time spent in each habitat, otolith growth rate and fish age (Miller 2011; Walther & Limburg 2012). Longer stays in new habitats (>14 days) and high otolith growth rates (usually a function of age) generally result in a detectable change in the element profile (Walther & Limburg 2012).

Different chemical markers can also be combined to provide a habitat specific "fingerprint" that allows researchers to address the issues of recruitment, connectivity and stock structure (Campana 1999). This technique is perhaps most suited for freshwater spawning species (resident and anadromous), as fresh water is chemically more diverse than seawater (e.g. Walther & Thorrold 2010; Zeigler & Whitledge 2011; Martin et al. 2013; Engstedt et al. 2014). However, marine applications on large spatial scales are also very common (e.g. Lara et al. 2008; Rooker et al. 2014). The applicability of this technique relies mostly on the chemical heterogeneity of the studied system(s); in fresh water, this is mostly a function of bedrock composition and age (Kennedy et al. 2000).

2. OBJECTIVES

The main objective of the present thesis was to study the use of fresh and brackish water during different life history stages of three freshwater fish species living in coastal waters of the Baltic Sea. While the methodological emphasis was given to the chemical composition of otoliths, their time-recording property was fundamental to this study and therefore also addressed in respect to stock management. An additional objective was to investigate the applicability of several chemical markers in different modelled systems and species.
The specific objectives of the thesis were to:

1. investigate the applicability of Sr:Ca and Ba:Ca profiles as tracers of salinity history (**I**, **II**, **V**, **VI**) and natal ^{87}Sr:^{86}Sr values as natural site-specific tags (**III**);
2. investigate the importance of freshwater spawning for two predatory (**I**, **II**, **VI**) and one prey species (**V**) living in coastal areas of the Väinameri Sea;
3. investigate the migratory patterns of two predatory (**I**, **II**) and one prey species (**V**) living in coastal areas of the Väinameri Sea;
4. investigate the age structure and growth parameters in one predatory (**II**) and one prey species (**IV**) using stained otolith thin-sections.

The study species were pike (*Esox lucius*), burbot (*Lota lota*) and ide (*Leuciscus idus*). The former two are predatory species and the latter is a prey species. Pike and burbot were chosen as model species because ecosystems of the Baltic Sea are currently strongly prey-fish dominated, and therefore predatory fish require special attention in management plans to increase top-down control in food webs. Pike also have significant commercial and recreational value, though burbot currently only have limited recreational value in the Väinameri Sea. Ide were chosen as a model species because they are the only prey-fish species in the Väinameri Sea whose population size has not increased in pace with other prey-fish species. Ide currently have some recreational value in the Väinameri Sea.

3. MATERIALS AND METHODS

3.1. Study species

Pike are a top-predator in the food chain and therefore important in structuring fish communities (Craig 1996). Pike can be found in a variety of habitats, from small freshwater ditches and ponds to brackish water seas such as the Baltic and Caspian (Westin & Limburg 2002; Pihu & Turovski 2003a; Bogutskaya & Naseka 2006). Although widely known as a freshwater species, pike have also established sympatric anadromous and sea spawning populations in the Baltic Sea (Erm et al. 1970; Westin & Limburg 2002; Engstedt et al. 2010; Jørgensen et al. 2010). In some areas of the Baltic Sea, the proportion of freshwater recruitment has decreased to 46% (Engstedt et al. 2010). Destruction or degradation of freshwater spawning areas (e.g. wetlands) is most likely the factor behind low freshwater recruitment, as it is a large problem throughout the region. For example, it is estimated that more than 90% of wetlands have been lost in the most exploited areas of Sweden (Nilsson et al. 2014). Pike start to spawn when the water temperature has risen to 4–6 °C; in the Baltic Sea region spawning takes place between late March and early June (Pihu & Turovski 2003a). Anadromous pike can mix with resident pike in freshwater spawning grounds (Müller 1986). The propensity of resident individuals spawning anadromous progeny (or *vice versa*) is unknown for pike, but can be significant in salmonids (Courter et al. 2013), which are the closest relatives to esocids (Ishiguro et al. 2003). The progeny of freshwater spawning pike descend to the sea at various ages and sizes, but >90% do so within their first three months and before reaching a total length of 60 mm (Müller 1986; Johnson & Müller 1978; Engstedt et al. 2010). Pike migrations in the Baltic Sea are mostly within a distance of 1–10 km from the natal river (Johnson & Müller 1978; Müller 1986; Karås & Lehtonen 1993). Natal homing in pike is well developed (Karås & Lehtonen 1993; Engstedt et al. 2014). The problems pike encounter in the sea relate to eutrophication driven problems in coastal spawning areas (Nilsson et al. 2004; Lehtonen et al. 2009), habitat destruction and overfishing (Kangur et al. 1982; Sundblad & Bergström 2014). In Estonia, inaccessibility of freshwater spawning areas due to natural blockage of river mouths and poaching of fish during spring spawning are also of major concern. Pike has significant commercial and recreational value (Pihu & Turovski 2003a; Lehtonen et al. 2009).

Burbot are commonly known as the only gadoid restricted to freshwaters (Stapanian et al. 2010). In Eurasia however, burbot also inhabit the brackish waters (e.g. the Baltic and Caspian seas, the Gulf of Ob) and undertake anadromous migrations to rivers and lakes (Müller & Berg 1982; Bogutskaya & Naseka 2006; Koporikov & Bogdanov 2011). Lehtonen (1998) even claimed that burbot can complete their life cycle solely in brackish water, although no supporting data was presented. The importance of freshwater spawning for

brackish water living burbot has not yet been quantified. Burbot spawn in winter (January-February) and young-of-the-year (YOY) hatch in spring (April-May) (Pihu & Turovski 2003b). The progeny of anadromous burbot inhabit freshwaters for 3–6 months prior to descending to the sea (Eriksson & Müller 1982). Burbot migrations in the Baltic Sea can exceed 20 km, but are mostly within 10 km of the natal river (Hudd & Lehtonen 1987). Natal homing is well developed in burbot (Hedin 1983; Hudd & Lehtonen 1987). Burbot living in the Baltic Sea reach sexual maturity at the age of 2–3 years (Lehtonen 1998). Burbot are an important top-predator in many cold water ecosystems and have moderate commercial and recreational value in several countries (Pihu & Turovski 2003b; Stapanian et al. 2010). The problems associated with Baltic Sea living burbot generally concern freshwater recruitment, as many spawning rivers have been polluted, acidified or habitat change has occurred (Hudd et al. 1983; Stapanian et al. 2010).

Ide are rheophilic cyprinid that occur naturally in the large lowland rivers and nutrient-rich lakes of Europe and Asia (Järvalt et al. 2003). However, large numbers of ide can also be found in the brackish coastal waters of the Baltic and Caspian seas (Järvalt et al. 2003; Bogutskaya & Naseka 2006). A population living near the Øresund Strait in the Baltic Sea are probably an example of ide living at the upper limit of their salinity tolerance (i.e. 10–20 ‰) (Cala 1975). Ide are known to spawn in rivers, lakes, estuaries, bays and reportedly even in open coastal areas of the Baltic Sea (Erm et al. 1970; Müller & Berg 1982; Järvalt et al. 2003), but the proportional importance of different spawning biotopes has not been quantified. Anadromous migrations to rivers and lakes may start under ice, with spawning beginning some days after ice breakup at water temperatures of 4–6 °C, usually in the middle of April (Järvalt et al. 2003). Spawning in flooded shallow areas lasts for only 3–7 days, after which adults migrate back to the sea (Järvalt et al. 2003). Ide larvae hatch at the beginning of May and they stay in fresh water for a year before descending to the sea (Cala 1975). Migrations in the sea can be relatively extensive, but homing seems to be profound (Johnson 1982). Ide growth in brackish waters is fast compared to freshwater resident populations and maturity is usually reached at the age of seven in both habitats (Oolu 1968; Järvalt et al. 2003). The growth rate of ide is one of the highest amongst cyprinid fishes, making ide a desirable target for commercial and especially recreational fisheries in several countries (Järvalt et al. 2003; Krejszeff et al. 2009). The problems associated with Baltic Sea living ide generally concern dysfunctional freshwater recruitment, as many spawning areas have been acidified (Eriksson & Müller 1982) or anthropogenic or natural habitat change has occurred (e.g. damming, ground uplift and dense vegetation at river mouths).

3.2. Study area and sample collection

The present thesis is based on field samplings conducted in the Väinameri Sea region (Fig. 1). The Väinameri Sea is a semi-enclosed sub-basin of the Baltic Sea, where seawater temperatures vary annually between 0–28 °C and duration of ice cover is 1–5 months. Surface salinities vary between 4–6 ‰ and average water depth is approximately 5 m (Kumari 1970; 1985). The Väinameri Sea is an important feeding and spawning area for many marine and freshwater fishes. Numerous freshwater rivers, creeks and ditches disembogue to the sea and serve as vital spawning areas for several anadromous fish species. Furthermore, multiple semi-enclosed shallow bays are flooded with fresh water in spring and also function as productive spawning areas (Ojaveer et al. 2003).

Fish were collected from various sites in and around the Väinameri Sea (Fig. 1). Juvenile pike were caught using electrofishing and beach seine from rivers and river mouths, respectively. The juvenile pike were then used to establish site-specific fingerprints to see if the study sites can be discriminated (**III**). For all study species, adult fish were obtained from fishermen or the

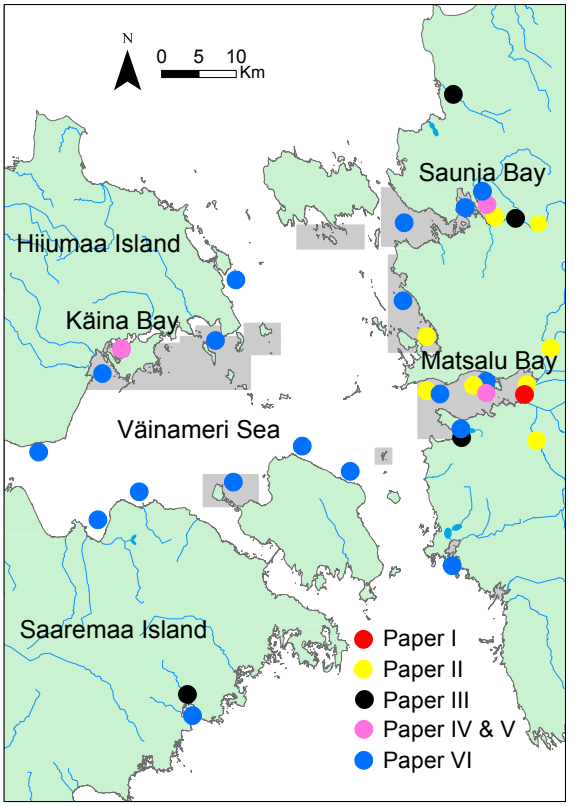

Figure 1. Study region and sampling sites of the present thesis. Grey shaded areas denote the brackish water spawning areas of pike and ide in the Väinameri Sea according to Erm et al. (1970).

archives of the Estonian Marine Institute. Additional sampling was conducted with gillnets and fykenets where needed. Fish total length (TL) in mm and sex were recorded for all individuals. Sagittal (pike, burbot) and lapillar (ide) otoliths were extracted from the fish, cleaned of adhering tissue and stored dry in microtubes for future analysis. Water samples were also collected throughout the Väinameri Sea to obtain information about the ambient environment. Water samples were filtered (0.45 μm) and acidified to pH 2 with nitric acid for future analysis.

3.3. Otolith preparation and analysis

Otoliths need to be processed to expose their growth history for age determination and chemical analyses. Before processing, both lapillar otoliths from ide were weighed to the nearest 0.1 mg. Subsequently, one otolith from each individual was embedded in epoxy resin and a frontal thin-section was obtained by manually grinding both sides of the epoxy block on a grinding machine. Silicon carbide sandpapers with grit sizes of P400 and P1200 were used and the process was stopped when the core was visible from one side. A final polishing was given with a grit size of P4000. The otoliths from burbot were prepared in a similar manner, but transverse thin-sections were obtained instead of frontal thin-sections. Pike otoliths were mounted (sulcus side up) onto a piece of glass slide or cover-slip using Crystal bond thermoplastic wax or superglue. Otoliths were then ground manually until the core was visible following the procedure described for ide. The obtained thin-sections were glued onto standard glass slides and stored in sealed plastic bags.

Before chemical analysis, all otoliths were ultrasonically cleaned for 10–15 minutes in ultrapure water and dried in a laminar flow hood. The chemical analyses of otoliths was conducted at Tallinn University of Technology (**I**) and Oregon State University (**II**, **III**, **V**, **VI**). Laser ablation was used in conjunction with inductively coupled plasma mass spectrometry (LA-ICPMS) to quantify the elemental composition of discrete parts of the otoliths (**I-III**, **V**, **VI**). External calibration was conducted using NIST 610 and 612 standards. The isotopic $^{87}Sr:^{86}Sr$ composition of otoliths (**III**) was quantified with a multi-collector LA-ICPMS. An in-house marine carbonate standard was used to monitor instrument accuracy and precision. Water samples were analysed in Tallinn University of Technology using the ICPMS device for solution analysis following the certified laboratory protocol.

Individual ages of fish were determined from the obtained thin-sections. In pike, the metapterygoid bone was also used for age determination. For clearing up the annuli in the otolith thin-sections burbot and ide otolith thin-sections were stained for 15 minutes in a solution of neutral red (1%), acetic acid (0.5%) and distilled water. This was done after the chemical analyses and resulted in significantly clearer annuli for age determination.

4. RESULTS AND DISCUSSION

4.1. Applicability of different chemical markers

Estonian freshwaters have significantly lower Sr:Ca values than the Baltic Sea (**I**, **II**, **V**, **VI**). This is further verified by both otolith data from several other species and the water chemistry of numerous freshwater bodies near the coast of Estonia (Matetski 2014; Taal et al. 2014; Rohtla, unpublished data). The Sr:Ca ratio of otoliths was a relatively straightforward proxy of salinity, at least for identifying hatching habitats and investigating major migrations between fresh and brackish water (i.e. the first seaward descent and spawning migrations to fresh water). Regarding Ba:Ca data in water and otoliths, the results were not that helpful for inferring migration patterns and identifying hatching habitats. The usually reported negative relationship between salinity and water Ba:Ca was not observed (**II**, **V**), possibly because the sampling protocol was rather temporally and spatially constrained. More importantly otolith Ba:Ca profiles of sea-caught adults did not indicate large scale variations and whilst of some use for burbot (**II**), were not useful for inferring ide movements (**V**). Similar results have also been observed in pike (Rohtla, unpublished data). The factors responsible for this are not known, but it can be hypothesised that the combination of Baltic Sea hydrology (low water retention times, large riverine runoff) and heavy eutrophication ($BaSO_4$ is associated with productivity (Stecher & Kogut 1999)), may result in almost equal Ba concentrations in the Baltic Sea and its freshwater basins.

Significant differences in juvenile pike otolith ^{87}Sr:^{86}Sr natal values were found among the study sites (**III**). This result further verifies the usefulness of this marker as a natal chemical tag (e.g. Walther & Thorrold 2010; Martin et al. 2013) and demonstrates its potential in the Baltic Sea. However, the use of additional chemical markers is advised, especially in cases where numerous (neighbouring) freshwater bodies are investigated. This is because the probability of overlapping chemical signatures increases with the number of study sites. The work on ^{87}Sr:^{86}Sr also pointed out some methodological issues. First, in cases where precocious freshwater emigration is common, care must be taken to ensure that natal fingerprints are not taken from the otolith region that contains marine material (**III**). This can happen when a temporally discrete spot or line is analysed (on sea-caught adult otolith) without accounting for the possibility that this individual may have left freshwaters unexpectedly early. As a result, pure seawater signal (easily recognisable) or a mixture of fresh- and seawater signals (false freshwater signal) could be obtained. Second, otolith cores should be avoided in chemical assays unless the core data can be easily omitted (e.g. as in core-to-edge scans) (**III**). Using temporally discrete spots and lines near the core may result in accidental (e.g. human or apparatus bias) sampling of the core, producing a chemical mixture of fresh- and seawater signals.

4.2. Importance of freshwater spawning

Eighty-nine per cent of adult pike (N=463) collected from brackish water hatched in fresh water (**I**, **VI**). This is nearly twice as many as reported from the eastern coast of Sweden (i.e. 46% (Engstedt et al. 2010)). The reasons behind this discrepancy are unknown, but it may be hypothesised that Estonian coastal freshwater bodies are sufficient in number and quality to allow for freshwater recruitment to strongly prevail. However, loss of freshwater habitat has also been significant in Estonia as multiple coastal rivers were channelized during the Soviet era. This is most pronounced on the islands of Hiiumaa and Saaremaa. The rivers located for example in the south-eastern part of Hiiumaa Island have low or nearly absent summer discharge rates and the river mouths are often blocked as a result of dense vegetation or ground uplift (Estonian Marine Institute, unpublished data). Deterioration in water quality is also likely, but has not been studied thoroughly. The poor environmental status of those rivers is also reflected in the hatching habitat data acquired from the adult fish sampled in the region: most of the individuals born in brackish water were collected from the south-eastern part of Hiiumaa Island (**VI**). These results coincide with the brackish water spawning areas of pike as reported by Erm et al. (1970), whereas in other areas no such agreement between studies was found. Therefore, it can be hypothesised that the prevalence of brackish water spawning has decreased in the Väinameri Sea region over the last 45 years. Our results strongly suggest that freshwaters are currently the main spawning habitat for pike in Estonian coastal waters (**I**, **VI**).

Several factors may hinder successful reproduction of pike in brackish waters. For example, deterioration of brackish water spawning grounds owing to eutrophication and egg predation by sticklebacks are known to negatively affect pike reproduction elsewhere in the Baltic Sea (Nilsson 2006; Eriksson et al. 2009). As eutrophication is pronounced (Martin 2007) and the sticklebacks abundant also in the Väinameri Sea (Estonian Marine Institute, unpublished data), these factors could be responsible for the small importance of brackish water spawning observed in the present thesis (**I**, **VI**). Additionally, food deficiency during the post-hatching period may be an important regulating factor of pike populations (Nilsson et al. 2004), although no such data is available for the Väinameri Sea. Alternatively, it could be that the sea-spawning and anadromous contingent of pike in the Väinameri Sea were fished-out in the early 1990s (Vetemaa et al. 2001) or earlier, with the sea-spawning population not (yet) having recovered due to a larger fishing toll. However, this is unlikely as the fishing pressure should be the same for anadromous and sea-spawning individuals.

The prevalence of brackish water spawning may be even lower than observed in the present thesis, as Johnson and Müller (1978) demonstrated that pike eggs spawned to the lowermost reaches of a river can drift to the (saline) estuary in large numbers, although unfortunately the fate of these eggs was not

addressed. Westin and Limburg (2002) found that the eggs of anadromous pike can hatch in ambient salinities of 0–6 ‰, but they did not investigate the salinity tolerance of larvae. Drift of freshwater spawned eggs to brackish water (or fresh water with high Sr:Ca ratio) may go unnoticed, as otolith Sr:Ca ratios will indicate such specimens as brackish water recruits. The same issue can occur with larvae that do not get enough time in fresh water to allow for the incorporation of a freshwater signal. Therefore, the proportion of brackish water recruits may be overestimated if the eggs and larvae drift to the estuary and it is also a source of recruitment. However, it is likely that the described phenomena are more an exception than a rule and therefore of marginal influence. This especially applies for eggs, as they require adhesion to vegetation for successful development (Craig 1996). Still, salinity tolerance of the eggs and larvae of freshwater spawning pike remains largely unquantified and should be thoroughly investigated in the future.

Ninety-six percent of sampled adult burbot (N=74) hatched in fresh water (**II**). There has been no prior explicit testing of spawning habitat preference of burbot in brackish seas. It has been suggested that sea-resident and anadromous forms coexist in the Baltic Sea (Lehtonen 1998), but this statement is based on two earlier studies that do not mention the possibility of brackish water spawning (Hudd & Lehtonen 1987; Müller 1987). The only evidence that slightly favours Lehtonen's (1998) sea-resident hypothesis is Hudd et al.'s (1983) study of newly hatched larvae from an area close to the mouth of the River Kyrönjoki, in which the authors argued that burbot probably spawned in the archipelago near the estuary and not in the river itself. However, the salinity regime of this rather closed system with large riverine runoff was not reported and it could be that the spawning areas contained fresh water as recently demonstrated by Asmala et al. (2014). Furthermore, this otherwise anadromous population was reportedly forced to spawn near the river mouth because the river was acidified (Hudd et al. 1983). Based on all the evidence, the life history of brackish water living burbot in the Väinameri Sea strongly points towards freshwater reproduction in normal situations. However, it seems that under special circumstances (e.g. river pollution, habitat destruction), burbot may spawn at the mouths of rivers (Hudd et al. 1983; Hudd & Lehtonen 1987). This may also be the case in the River Taebla (Saunja Bay), because in this present study no YOY burbot were recorded in the river, despite the catching of pre- and post-spawning adults at the river mouth. However, the Sr:Ca profiles of adults indicated juvenile being reared in the river water and not in the higher Sr:Ca water ratios of Saunja Bay (**II**). It may be that spawning occurs and juveniles live only in the deeper parts of the river, and electrofishing was not effective in catching individuals at such depths. The environmental status of the River Taebla should be thoroughly investigated in the future, as some other anadromous species have also disappeared from the river (e.g. ide (**V**)).

Possibly all, but at least a large majority of the ide collected from the Väinameri Sea were spawned in fresh water, however the choice of spawning

biotope had shifted from rivers to *seasonally freshwater bays* in some locations (**V**). We found that 88% (N=22) of individuals from Matsalu Bay, 33% (N=9) of individuals from Saunja Bay and 0% of individuals from Käina Bay were spawned in rivers. The remainder of the fish in each site were spawned in freshwaters with moderate Sr:Ca values (seasonally freshwater bays) or in brackish waters (N=80 in total) (**V**). While the quantified natal Sr:Ca values were generally higher than the riverine threshold of 0.6 mmol/mol (except in Matsalu Bay), water analyses indicated that the waters of Käina and Saunja bays also had higher ambient Sr:Ca ratios than the rivers (**V**). This was because these bays are often flushed with brackish water during summer-autumn-winter (inducing permanently higher Sr:Ca ratios owing to sediment deposition) and only contain fresh water during spring when spawning occurs. These results suggest that for ide spawning conditions in the rivers have deteriorated.

Most likely two factors have contributed to the obvious decline of river-running ide. First, some rivers are physically inaccessible to ide as a result of dense vegetation and ground uplift at the river mouth and/or the presence of beaver dams. Dense vegetation most likely results from river channelization and wetland destruction, which leads to low water retention time in tributaries and the flushing of nutrients to the river mouth, where they accumulate and support rich plant growth (Hoffmann et al. 2000, Vahteri et al. 2000; Verhoeven et al. 2006). Second, the quality of river water and habitat has deteriorated to an extent which makes it impossible for ide to (successfully) spawn in the river. However, it needs to be stressed that no direct evidence of the second factor currently exists. In lakes and rivers ide usually spawn in flooded shallow areas on dead vegetation (Järvalt et al. 2003), i.e. conditions which are lacking in channelized rivers. Furthermore, some of the rivers in the south-east of Hiiumaa Island have unfavourable hydrology and water quality: they often cease flowing and become fragmented, resulting in oxygen deprivation and water blooms (Rohtla, unpublished data). Also, ide may simply have become adapted to spawning in seasonally freshwater bays or even brackish water, similar to e.g. ruffe, *Gymnocephalus cernua* (Vetemaa & Saat 1996), but this was not seen in the present thesis in systems where rivers are in seemingly good condition (e.g. Matsalu Bay). Clearly, all of these issues need to be addressed in the future if good status of spawning rivers is desired. The results of the present thesis do not support the conclusions of previous research that suggested ide can also spawn in the brackish waters of the Väinameri Sea (Erm et al. 1970). It should be noted that this historical statement was based on inconclusive data and anecdotal evidence. However, it may well be that brackish water spawning *did occur in the past* or it is just not that successful in terms of recruitment.

In conclusion, the present thesis demonstrates that the investigated freshwater fishes of the Väinameri Sea largely depend on freshwater spawning. This indicates that the studied species have not (yet) adapted to spawning in the brackish waters of Baltic Sea like, unlike many others (e.g. perch *Perca fluvitilis*, pike-perch, ruffe, white bream *Blicca bjoerkna*) which have. For the

investigated species (pike, burbot and ide) therefore, attention should be paid to conserving and restoring pristine freshwater habitats. It is easier to concentrate these actions on freshwater rather than brackish water habitats, because eutrophication is more pronounced and permanent in the latter (HELCOM 2010). For example, river and wetland restoration can enable fish to recolonize deserted spawning areas and increase water retention time in rivers, which should eventually reduce the nutrient load to the sea by incorporating nutrients to freshwater primary production instead (Nilsson et al. 2014). Furthermore, increased numbers of predatory fish should lead to decreased phytoplankton concentrations in the sea – an indirect positive effect through food chain (Eriksson et al. 2009; Ljunggren et al. 2010). According to the results of the present thesis and the study of Engstedt et al. (2010), pike seem to be rather flexible in terms of their spawning habitat preferences. Although there are no other comparable studies for burbot and ide, it would seem based on the results of the present thesis that individuals of these species residing in the Väinameri Sea mainly depend on freshwater spawning. A couple of burbot and ide however did display signs of hatching in a brackish water environment. However, these specimens could have been drifters or their chemical profiles methodological artefacts (**II**, **V**). The current salinity regime in the Baltic Sea may change in the future, as the salinities are projected to drop further due to increases in precipitation (Kjellström & Ruosteenoja 2007; Meier et al. 2012; cf. Ojaveer & Kalejs 2012). As a result, brackish water spawning may become more widespread, especially in areas where freshwaters are inaccessible or of poor quality.

4.3. Migration patterns

Pike migration patterns were diverse, even within the relatively small geographical range used in the present thesis (**I**). Seventy-four per cent of the pike sampled (N=28) left the Matsalu Bay freshwater nursery grounds during their first growth season, but the timing of their seaward migration was less fixed (**I**) than previously shown for small coastal rivers (Johnson & Müller 1978; Engstedt et al. 2010; Nilsson et al. 2014). The results of the present thesis for Matsalu Bay showed that on average YOY pike emigrated to the sea at 3 months of age and 8 cm in total length (**I**). Johnson and Müller (1978) recorded the descent of YOY pike with a fry trap and found that approximately 80% of the individuals had left the stream within one month, but the emigration period lasted until late August when the fish had reached a total length of 8 cm. Similarly, using fry traps in the mouths of three rivers Nilsson et al. (2014) found that 80–95% of YOY pike emigrated to the sea within the first month at total lengths of 1–7 cm. The observed differences between the results of the present thesis and the three aforementioned studies are most likely due to different study systems. The three aforementioned Swedish studies investigated

small coastal rivers, where space and food is limited as water levels decrease after pike spawn in spring. Therefore, most of the pike are forced to descend to the sea, where food resources are richer and the habitat less limited (Müller 1986). Presumably, this is not the case in Matsalu Bay, where the freshwater nursery areas are large (fed by multiple rivers) and food is plentiful (Vetemaa et al. 2006). It should be noted that similar to Engstedt et al.'s (2010) findings, present study also observed few individuals that had emigrated to the sea at an older age and greater size than the average (**I**).

High levels of plasticity were observed in pike seaward migration patterns and habitat selection at the sea (**I**). It seemed that some freshwater born Matsalu Bay pike emigrated to higher salinities rather fast, as displayed by a sudden increase in their otolith Sr:Ca profiles. Others took their time and moved towards higher salinities at a slower pace (Fig. 2a, b). There was also significant variation in the maximum values of Sr:Ca amongst individual profiles, suggesting that pike in this system differed in terms of their habitat choice. For example, some individuals were clearly freshwater residents, whereas others most likely stayed in the bay or moved to the Väinameri Sea. It is generally accepted that pike migrations in the Baltic Sea do not exceed 1–10 km and strong homing behaviour exists (Müller 1986; Karås & Lehtonen 1993; Engstedt et al. 2014). However, natal fingerprinting of pike in the Väinameri Sea has revealed that migration distances may be significantly higher (Rohtla, unpublished data). Therefore it is likely that anadromous individuals make use of the whole Matsalu Bay area (and probably even beyond) and home towards their freshwater spawning areas from various distances.

Burbot demonstrated considerable life history plasticity in terms of age and length at first freshwater emigration and at maturity (**II**). Most of the burbot descended to the sea during late winter and spring the year following their birth. Otolith Ba:Ca profiles indicated that this descent may be triggered by elevated river discharge (Fig. 2c). A new life history strategy was also observed, i.e. precocious migrants that had emigrated to the sea during the first or second month post-hatch (Fig. 2d). All this contrasts to earlier fry trap studies conducted in the River Ängerån (Baltic Sea), which found that juvenile emigration occurred from late August to late January (Eriksson & Müller 1982). The reasons behind this discrepancy are not known. It might be that similar to pike in River Ängerån (Johnson & Müller 1978), decreased water levels, together with high densities and the increased food demand of YOY, caused burbot from the River Ängerån to descend to the sea earlier than in the systems studied in the present thesis. However, river discharge rates are almost equal between the Ängerån and Taebla rivers (i.e. below 1 m^3 s^{-1} during the period outside of spring flooding), but higher and more versatile (i.e. 2–25 m^3 s^{-1}) in the rivers that drain into Matsalu Bay. Therefore, the wide emigration period of burbot observed in the present thesis is more comprehensible in Matsalu Bay, as it is fed by multiple rivers with various discharge rates.

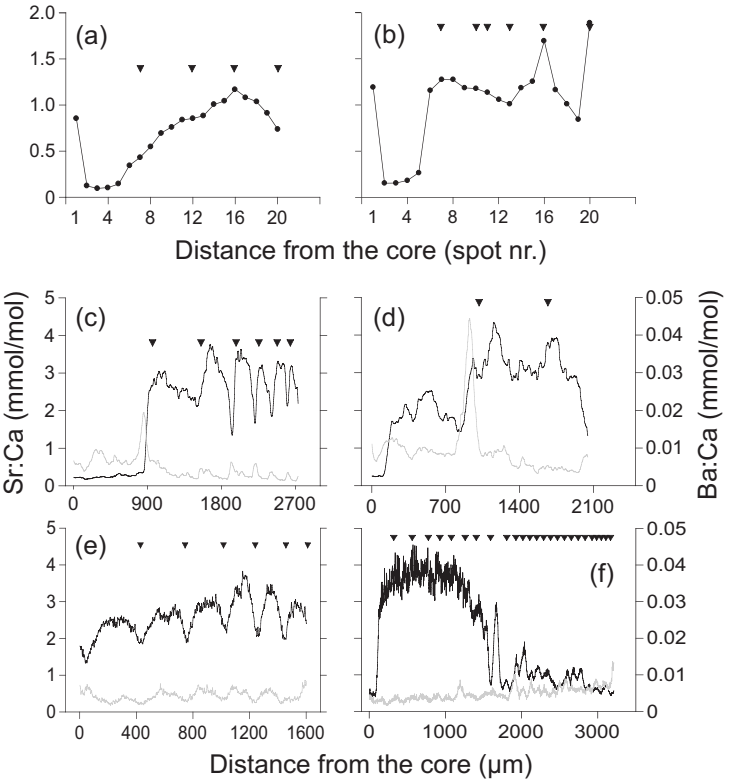

Figure 2. Representative Sr:Ca (black lines) and Ba:Ca (grey lines) profiles of the species investigated in the present thesis: (a–b) pike; otoliths were ablated with 20 consecutive spots, (c–d) burbot; otoliths were ablated with a continuous line-scan mode, (e–f) ide; otoliths were ablated with a continuous line-scan mode. Note the high Sr:Ca core values in pike, which represent maternal contribution to the developing egg, and indicate that the mothers of particular specimens were anadromous individuals (Kalish 1990). Triangles denote the annuli.

There is also the question of whether precocious migrants represent an example of life history plasticity or were they simply flushed to the sea with lowering water levels? Burbot is a winter spawning species and this limits the number of waterbodies suitable for spawning due to low water levels in winter. In spring many small creeks and ditches, which are during the rest of the year mostly dry, become available for spring spawners (e.g. pike), but water levels soon reduce and force larvae to descend to the sea (Nilsson et al. 2014). Therefore, the chance of burbot spawning in waterbodies that lose most or all water in late spring or early summer (and induce precocious migrations) is minimal. However, in the present thesis a small number of landlocked burbot larvae were caught during July 2014 in Sauemeri near Matsalu Bay (Fig. 1), which is a large plain that floods annually in spring, but is only connected to the sea for a short time and virtually dries up in summer. This means that in winters with high

riverine runoff, burbot may spawn in hydrologically extremely labile waterbodies. In Sauemeri, the caught larvae probably had a narrow emigration window during spring (depending on hatching time). However, the precocious migrants observed in the present thesis resided in fresh water for longer periods than the narrow emigration window at Sauemeri, which may suggest that these fish were not from such labile waterbodies and were "true" representatives of burbot life history plasticity. These issues need to be addressed more thoroughly in the future. Overall, the results of the present thesis support and add to Eriksson and Müller's (1982) conclusion that juvenile burbot have a less narrow freshwater emigration period than other freshwater species of the Baltic Sea.

Most of the adult burbot had returned to freshwater during the second or third year of their life and therefore likely reached maturity (**II**). Same age at maturity has been reported from Matsalu Bay tributaries (Erm et al. 2002) and the coast of southern Finland (Lehtonen 1998). However, 15% of sampled individuals (N=67) also displayed signs of late maturity, i.e. maturity was reach 1–3 years later than average (**II**). Late maturing burbot have also been reported in Lake Peipus (Pihu & Pihu 1973). Late maturation (especially in anadromous burbot) may be adaptive as it enables more investment in growth and eventually leads to greater fitness in terms of higher fecundity (females) and advantages in sexual selection (males). Previous researchers have also suggested that burbot, when in a poor nutritional state, may have rest years between spawning seasons (see Pulliainen & Korhonen 1993 and references therein). However, sterility of burbot from the Bothnian Bay was caused by effluents from pulp mills (Pulliainen et al. 1999). In the present thesis no rest years were evident in the Sr:Ca profiles of burbot from the Väinameri Sea. Once spawning migrations started they occurred annually (Fig. 2c).

All of the sampled ide (N=111) emigrated to the sea during the first few months of their lives, but 95% did so during the first month post-hatch (**V**). This is intriguing new knowledge as juvenile ide were previously known to spend a year in the rivers before migrating to the sea (Cala 1975; Kokko & Mäkinen 1981; Erm & Kangur 1985). However, this historical knowledge is based on an anadromous ide population spawning in the River Kävlingeån, but living in southern part of the Øresund Strait where salinities vary from 10–20 ‰ (Cala 1975). Ide living in such conditions are probably at their salinity tolerance limit. Therefore, it is reasonable to expect that juvenile ide destined to descend to higher salinities need more time to grow in fresh water. This is because larger individuals are generally more capable of adapting to the increased osmoregulatory demands (Beckman et al. 2003; Mojazi Amiri et al. 2009). Unfortunately, Cala's (1975) results have been adopted at the scale of the entire Baltic Sea and are often cited as a universal trait of ide life history (e.g. Kokko & Mäkinen 1981; Erm & Kangur 1985). Salinity in most of the Baltic Sea is below 8 ‰ and such salinities seem tolerable to ide during early life stages. Why then do juvenile ide emigrate from freshwaters at such a young age and small size as observed in the present study? One possible explanation is that

juvenile ide need more food due to an inherently higher growth rate compared to other cyprinids (Järvalt et al. 2003). Faster growing individuals from other species are known to migrate significantly earlier than slower growing conspecifics (e.g. Økland et al. 1993; Benjamin et al. 2014). Alternatively, juvenile ide may compete for nursery grounds with other cyprinids and this forces ide to descend earlier. For example, juvenile roach remain in their natal areas in summer and start their seaward migration 2–7 months post-hatch (Eriksson & Müller 1982). Furthermore, the most abundant ide stocks in Estonia currently occur at Hiiumaa Island where roach are practically absent (except in the northern side of the island). Conversely the most abundant roach stocks occur in Matsalu and Saunja bays where ide are practically absent (Eschbaum et al. 2014).

Otolith Sr:Ca profiles indicated that after arriving to the sea, ide display a variety of movement patterns (**V**). First, a significant part of the stock undertook non-reproductive migrations back to the freshwaters during the following spring(s) (Fig. 2e). This result was supported by information from anglers, who reported catching juvenile ide in rivers during the annual spring spawning migration of adult roach and ide. While similar movements have been documented in juvenile anadromous herrings (Limburg 1998), the adaptive value of this phenomenon remains unknown. The most likely explanation is that freshwater migration by juveniles is the result of schooling, whereby juveniles move to the spawning grounds with adults (i.e. a type of collective navigation (see Berdahl et al. in press.)). Alternatively, it can be hypothesised that juvenile ide undertake spring migrations to fresh water in order to feed at optimal thermal conditions, as the water temperature in freshwater wetlands, rivers and bays rises quickly in spring. Second, individual ide differed in terms of their length of stay in fresh water (either during spawning or non-reproductive migrations), as evidenced by the number and extent of Sr:Ca nadirs (Fig. 2e, f). Compared to other freshwater species living in the Baltic Sea, ide are considered rather fast spawners (i.e spawning is completed usually in 3–7 days (Järvalt et al. 2003)) and this may contribute to the absence of Sr:Ca nadirs in many individuals. Third, a clear habitat switch was observed during the adult life phase of 10 Matsalu Bay ide (Fig. 2f). These individuals probably inhabited an environment with higher Sr:Ca (e.g. the Väinameri Sea or the outer reaches of Matsalu Bay) during the first part of their lives, but moved to lower Sr:Ca environment (e.g. the inner reaches of Matsalu Bay) later in life. The reasons behind this behaviour are unknown, but it may be that the release from predation pressure enabled those fish to utilize the shallower inner parts of the bay, where competition for food is lower and migration to spawning areas shorter (Vetemaa et al. 2006).

In conclusion, the present thesis has demonstrated that otolith microchemistry can provide a wealth of new information on fish migration patterns that is otherwise difficult or impossible to obtain. Remarkable levels of life history and behavioural plasticity were observed, both within and among species. Our results

add to the plethora of studies that have shown the movement patterns of fishes are complex (e.g. Tsukamoto et al. 1998; Daverat et al. 2012; Shrimpton et al. 2014). This life history plasticity is most likely an evolutionary buffer against an unpredictable environment (Crozier & Hutchings 2014) and this needs to be accounted for in management and conservation policies.

4.4. Age structure and growth parameters

Burbot with a history of being reared in brackish water demonstrated surprisingly fast growth rates (**II**). The age structure of Saunja and Matsalu bay stocks was dominated by individuals of two and three years old. Overall, growth rate of anadromous burbot investigated in this thesis was equal to or even higher (in younger age groups) than freshwater resident burbot living in Lake Peipus and Lake Võrtsjärv (Haberman et al. 1973) (Table 1). Age and growth rate of burbot living in the Baltic Sea has rarely been investigated. To our knowledge, the only available reference is a paper by Lehtonen (1973). Compared to the datasets of Lehtonen (1973) for burbot collected at Tvärminne (Finland), Matsalu Bay burbot showed similar growth rates, whilst growth rates of Saunja Bay burbot exceeded both (Table 1).

The superior growth conditions in brackish waters compared to coastal rivers was best exemplified by a freshwater resident burbot caught in the upper reaches of the River Taebla (which disembogues to Saunja Bay): it took eight years for this individual to reach a TL of 45 cm, whereas the anadromous individuals downstream reached this length in just three years (**II**). Anadromous behaviour can therefore be regarded as highly adaptive in small rivers, where conditions do not allow for high growth rates.

Regardless of the fast growth rate of anadromous burbot, individuals larger than 1.5 kg are rare and reported catches from the Väinameri Sea low, averaging less than one ton per year (Armulik & Sirp 2013). At the same time in Lake Peipus burbot reach sizes up to 5 kg and the reported catches are relatively high, averaging 50 tons per year (Saat et al. 2014). What factor(s) causes such differences? It can be argued that burbot is a freshwater fish and as such is better adapted to living in fresh than brackish water. However, high growth rates of anadromous burbot do not support this. Instead, one such factor might be the minimum allowable catch size in effect for Lake Peipus and Lake Võrtsjärv (TL 40 cm), but unregulated in all other waterbodies in Estonia, including coastal waters. Furthermore, burbot suffer under strong predation pressure from cormorants (*Phalacrocorax carbo*) in the Väinameri Sea (Eschbaum et al. 2003). Based on the growth rate data reported in the present thesis, it is likely that many Väinameri Sea burbot are caught (by humans or birds) before they can reproduce. To alleviate anthropogenic pressure, a minimum size limit (e.g. TL 40 cm) should also be established for coastal waters and lower reaches of coastal rivers. This is reasonable as the current

ecosystem state is strongly prey-fish dominated and other coastal predatory fishes in Estonian seas (pike, perch, pike-perch) already have minimum allowable size limits.

Table 1. Mean total length (mm) at age data for burbot collected at several coastal Baltic Sea sites and two freshwater sites. Numbers in parentheses indicate the sample size of respective age groups per site (note the small sample sizes in some age groups). The total length of most Matsalu Bay burbot was derived from back-calculation of otolith radii (**II**). Females and males were combined for each age group.

Age (years)	Tvär-minne (Lehtonen 1973)	Inkoo (Lehtonen 1973)	Helsinki (Lehtonen 1973)	Saunja Bay (**II**)	Matsalu Bay (**II**)	Lake Võrtsjärv (Haberman et al. 1973)* N=148	Lake Peipus (Haberman et al.1973)* N=202
1	–	–	–	–	191 (2)		190
2	–	–	–	362 (18)	353 (6)	304	333
3	368 (8)	395 (1)	405 (2)	440 (13)	388 (13)	389	366
4	433 (15)	490 (1)	–	513 (3)	444 (8)	481	453
5	485 (15)	–	–	420 (1)	451 (1)	506	542
6	524 (36)	–	–	–	516 (2)	596	575
7	565 (8)	740 (1)	670 (2)	–	530 (2)	624	618
8	652 (4)	–	680 (2)	–	–	629	674
9	–	–	–	–	–	–	729
10	–	–	–	–	–	–	753

* Total lengths calculated from standard lengths with a conversion factor of 1.066.

Age structure of ide varied significantly amongst individuals from Käina, Matsalu and Saunja bays **(IV)**. Käina Bay adults had the youngest age structure, as evidenced by the prevalence of 5–7 year old adults. The average age of adults in Matsalu and Saunja bays was 11 and 16 years respectively **(IV)**. In Käina Bay the observed age structure was to be expected, because the spawning stock is abundant and healthy with no apparent recruitment failures (Eschbaum et al. 2014). Both commercial and recreational fishermen exploit the Käina Bay ide spawning stock, which is probably the most numerous in Estonia (although fishing in the bay itself is prohibited). The current situation in the historically important ide spawning areas of Matsalu and Saunja bays is quite the opposite, with adult and especially juvenile fish rare (Eschbaum et al. 2014). The old-aged spawning stock and low abundance of ide indicate serious recruitment problems in Matsalu and Saunja bays. However, the specific factor responsible for recruitment failures is not known. Finding the factor responsible is particularly intriguing regarding Matsalu Bay, where other species (including

cyprinids) seem to reproduce successfully in the wetlands and rivers connected to the bay (Eschbaum et al. 2014).

Ide age range was unexpectedly high at all three study sites. Otolith thin-sections were used to record a maximum age of 29 years (**IV**), which is to the best of our knowledge the highest reported age for ide in the species' range. This is interesting as previous researchers from Estonia have recorded a maximum age for ide of 15 years (reviewed by Järvalt et al. 2003). Other studies could have underestimated ide ages because they used scales. Scales often underestimate the true age (Francis et al. 1992; Yule et al. 2008) and based on my own personal experience I believe ide are far harder to age with scales than using otolith thin-sections. Alternatively, this discrepancy in ages may be a result of altered population dynamics owing to modifications in environmental conditions and/or fishing pressure. This is supported by the collapse of ide-targeted commercial fisheries during the late 1980s (i.e. the period when the oldest fish in the dataset of the present thesis were born) and recruitment failures in some stocks as demonstrated in the present thesis.

4.5. The concept of anadromy

It has come more evident that the current definitions of diadromous fish (McDowall 1988; Elliott et al. 2007) are idealized and often open to subjective interpretations. The current terminology does not fully define so called "border line" cases, or novel fish migratory strategies that have been revealed with the help of new methods and do not fit with the traditional terminology (Tsukamoto et al. 1998; Thibault et al. 2007; Jensen & Rikardsen 2008; Davidsen et al. 2014; Smith & Kwak 2014). Therefore, there is an urgent need for a comprehensive contemporary terminology of fish migration types, though this will be a difficult task. My opinion based on research of freshwater fish in the Baltic Sea is that it cannot be done in a simple manner – there are just too many variations of migratory life histories. First, it needs to be decided whether to regard brackish water living, but freshwater spawning fishes as anadromous or not? I agree with McDowall (1988), who states in his fascinating book on diadromous fish that Baltic Sea salmon and river-run whitefish are diadromous, although only marginally. This means that sea salinity levels are not a factor in defining anadromy. So what is? According to McDowall (1997), diadromous migrations are regular, physiologically mediated movements that occur at predictable life history phases, involve *most* members of a species' populations and are *usually* obligatory. However, the words in (my) italics are ambiguous and can be variously interpreted. For example, multiple freshwater fishes living in the Baltic Sea (and most likely the Caspian Sea) fit this profile! McDowall (1988) regarded the Baltic Sea freshwater spawning cyprinids as "primarily freshwater fish who venture into the brackish water". I cannot agree with McDowall on this, because it was known even then that cyprinids and many other species do not

simply “venture” to the sea (e.g. Müller & Berg 1982). Of course, the degree of anadromy varies within and among species, as also shown in the present thesis. Therefore, I propose that two modes of anadromy should be distinguished in Baltic Sea freshwater spawning fish: 1) obligate anadromy (i.e. all populations and individuals within a species are anadromous, e.g. river lamprey *Lampetra fluviatilis*, Atlantic sturgeon *Acipenser oxyrinchus*); 2) facultative anadromy (i.e. most or some populations or individuals within a species are clearly anadromous while others are not, e.g. pike, brown trout *Salmo trutta*, Atlantic salmon *Salmo salar*) (Table 2). Facultative diadromy has been increasingly described in many species from different parts of the world (Tsukamoto et al. 1998; Howland et al. 2001; Hughes et al. 2014; Mai et al. 2014).

Second, in some countries (especially Estonia) the word “semi-anadromous” (*poolsiirdekalad*) is used to refer to species that *ascend the rivers from brackish waters* (Masing 1992). There is a clear contradiction in this definition as anadromous Baltic Sea salmon, seatrout and river lamprey should therefore also be referred to as semi-anadromous. However, they are not, and the term “anadromous” (*siirdekalad*) is widely used (Ojaveer et al. 2003). Therefore I propose to avoid the use of the term “semi-anadromous” in the context of the salinity of sea water and freshwater fish. We should instead categorize all freshwater spawning species as obligatorily or facultatively anadromous and use the term “semi-anadromous” exclusively for species whose spawning run from the sea extends only as far as the upper estuary, but not to fresh water (Elliott et al. 2007).

Table 2. Life history types of the fishes inhabiting the Baltic Sea that are known to spawn in fresh water.

	Species	Life history type(s)
Obligate anadromy	River lamprey, *Lampetra fluviatilis*	Anadromous (Saat et al. 2003)
	Atlantic sturgeon, *Acipenser oxyrinchus*	Anadromous (Paaver 2003)
	Twaite shad, *Alosa fallax*	Anadromous (Thiel et al. 2008)
Facultative anadromy	Atlantic salmon, *Salmo salar*	Mostly anadromous, but landlocked potamodromous populations and precocious sneaker males exist (Kangur et al. 2003a)
	Brown trout, *Salmo trutta*	Anadromous*, potamodromous (Järvekülg 2003; Kangur et al. 2003b)
	Whitefish, *Coregonus lavaretus*	Anadromous, fully marine, potamodromous (Sõrmus & Turovski 2003; Huuskonen et al. 2012)
	Smelt, *Osmerus eperlanus*	Fully marine, anadromous (Špilev & Turovski 2003)
	Pike, *Esox lucius*	Anadromous, fully marine, potamodromous (Pihu & Turovski 2003a; Jørgensen et al. 2008; Engstedt et al. 2010; **I**, **VI**)
	Vimba bream, *Vimba vimba*	All Baltic Sea living populations are anadromous, inland population are potamodromous (Erm et al. 2003a)
	Roach, *Rutilus rutilus*	Fully marine, anadromous, potamodromous (Eriksson & Müller 1982; Vetemaa et al. 2003; Härmä et al. 2008)
	Dace, *Leuciscus leuciscus*	Anadromous, potamodromous (Johnson 1982; Pihu & Turovski 2003c)
	Ide, *Leuciscus idus*	Anadromous, potamodromous (Müller & Berg 1982; Järvalt et al. 2003; **V**)
	Burbot, *Lota lota*	Anadromous, potamodromous (Johnson 1982; Paragamian & Wakkinen 2008)
	Three-spined stickleback, *Gasterosteus aculeatus*	Fully marine, anadromous, potamodromous (Johnson 1982; Saat & Turovski 2003)
	Perch, *Perca fluviatilis*	Fully marine, anadromous, potamodromous (Johnson 1982; Pihu et al. 2003; Tibblin et al. 2012)

* Arguably can also spawn in brackish waters, most likely in river mouths (Limburg et al. 2001).

SUMMARY

The fish fauna of the brackish Baltic Sea is composed of species of marine and freshwater origin. Although many of them live at their physiological limits in terms of salinity, the waters are enriched with nutrients and support a highly productive ecosystem. For freshwater species the low salinity of the Baltic Sea provides superior feeding conditions, a vast habitat and for some species even spawning areas. However, several species still depend on freshwater spawning and undertake anadromous migrations back to their natal habitats. This means that different coastal rivers, lakes, creeks and ditches serve as vital spawning and nursery areas for multiple brackish water living freshwater fishes. The state of coastal freshwater fish stocks largely depends on the accessibility and environmental health of these waterbodies – characteristics that often suffer owing to anthropogenic factors. However, the importance of freshwater spawning for brackish water living freshwater species is largely unquantified. Not much is known about their movement patterns, recruitment processes, age structure and growth rates. Elucidation of these issues should result in a better understanding of species ecology and population dynamics – knowledge that is vital for developing appropriate management plans and conservation actions.

The main objective of the present thesis was to study the use of fresh and brackish water during different life history stages of freshwater fishes that inhabit the coastal waters of the Baltic Sea. Although methodological emphasis was given to otolith microchemistry, otolith time-recording property was fundamental to the present study and was also thoroughly addressed. The specific objectives of the present thesis were to: (1) evaluate the applicability of different chemical markers in the context of the Väinameri Sea region and study species (**I**–**III**, **V**, **VI**); (2) investigate the importance of freshwater spawning in brackish water living pike (*Esox lucius*) (**I**, **VI**), burbot (*Lota lota*) (**II**) and ide (*Leuciscus idus*) (**V**); (3) investigate migration patterns between fresh and brackish water in pike (**I**), burbot (**II**) and ide (**V**); (4) investigate the age structure and growth rate in the sampled burbot **(II)** and ide (**IV**) stocks using stained otolith thin-sections. Most of the fish samples were collected in the Väinameri Sea region. Chemical analyses of otoliths were conducted with laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS).

The results of water and otolith analyses demonstrated that otolith Sr:Ca is a reliable marker for determining hatching habitat (i.e. fresh or brackish water) and inferring movements between Estonian freshwaters and the brackish waters of the Baltic Sea (**I**, **II**, **V**). The same conclusion could not be drawn for Ba:Ca, as it demonstrated no clear relationship with salinity (**II**, **V**) and it was therefore concluded that this marker only has a limited value in our study system. Otolith ^{87}Sr:^{86}Sr natal values demonstrated great potential in discriminating among pike natal areas (**III**). It was concluded that the otolith ^{87}Sr:^{86}Sr natal marker could be a powerful tool to study the natal origins of freshwater spawning fish in the Baltic Sea at local and regional scale. However, it is also advised to use additional

chemical markers in cases where numerous (neighbouring) freshwater bodies are studied.

Present thesis demonstrates that fresh water is the main spawning habitat and recruitment source for the studied species in the Väinameri Sea region (**I**, **II**, **V**, **VI**). Pike were most flexible in terms of spawning habitat, with an average of 11% of individuals of brackish water origin (**I**, **VI**). Regarding burbot and ide, brackish water hatching could be considered only in the case of a few individuals (**II**, **V**). The likelihood and importance of brackish water spawning for the studied species is even more diminished if the possibility of eggs and/or newly-hatched larvae drifting from freshwater spawning areas to brackish water is considered. The possibility of the latter scenario however, remains to be tested. In general, the results of the present thesis do not support previously published suggestions that numerous pike and ide spawning areas exist in the brackish waters of the Väinameri Sea and that burbot can spawn in brackish environments.

The studied species displayed considerable life history plasticity in terms of age and size at first freshwater emigration, age and size at maturity, and overall migratory patterns. Most of the anadromous pike from Matsalu Bay emigrated from freshwaters during their first growth season, but age and size at emigration was greater and less concentrated than previously shown for small coastal rivers (**I**). This was most likely the result of the vast nursery grounds and rich food resources that are available in the estuaries and wetlands of Matsalu Bay. After the onset of emigration, the same individuals displayed variable seaward migration patterns and habitat selection at sea. Burbot showed considerable variation in age and size at first freshwater emigration and at maturity (**II**). Most of the burbot descended to the sea during late winter and spring the year following their birth. Otolith Ba:Ca profiles indicated that this descent may be triggered by elevated river discharge. A new life history strategy of burbot was also observed: precocious migrants, which emigrated to the sea during the first or second month post-hatch. Most of the burbot reached maturity and made their first freshwater spawning migration during the second or third year of their lives, but there were also some individuals that exhibited delayed maturity and matured 1–3 years later. Regarding ide, an unexpectedly precocious freshwater emigration was documented in all of the individuals analysed and afterwards diverse migration patterns often occurred (**V**). Until now it was thought that ide reside in fresh water for a year and then descend to the sea. Present thesis demonstrates that all ide descend to the sea during the first or second month post-hatch in the Väinameri Sea. An interesting migratory phenomenon was also documented: juvenile ide undertook non-reproductive freshwater migrations in spring, most likely following the spawning adults. Furthermore, a clear habitat shift towards less saline waters was observed in multiple adult ide from Matsalu Bay, possibly indicating a release from predation pressure as the ide grow larger.

Burbot and ide age and growth rate data revealed some unexpected results. Burbot from Matsalu and especially Saunja bays demonstrated some of the highest growth rates ever recorded in the Baltic Sea and its freshwater basins (**II**). The age structure of the two stocks was dominated by two and three year old individuals. Regardless of their fast growth rate in the sea, abundances and catches of burbot are low compared to the Lake Peipus freshwater population. A minimum allowable catch size (e.g. TL 40 cm) should be established in the coastal waters and the lower reaches of coastal rivers. Regarding ide, the results of the present thesis indicate that age structure varied significantly among the spawning stocks of Käina, Matsalu and Saunja bays (**IV**). Käina Bay ide stock had the youngest age structure of the three bays, as evidenced by the prevalence of 5–7 year old adults. Matsalu and Saunja bays were dominated by significantly older individuals. We also observed a wide age range at all three sites and recorded a new maximum age (29 years) for ide. Variable ide age structure among sites was also reflected in the population dynamics of spawning stocks: juvenile and adult fish were abundant in Käina Bay, whereas they were low numbered in Matsalu and Saunja bays. This indicates that serious recruitment problems occur in the latter two (formerly important) ide spawning areas.

The knowledge gained in this thesis could be useful for resource management and conservation and restoration actions. **First**, the fact that the large majority of individuals studied were recruited from fresh water draws attention to the importance of this habitat in the life cycle of some coastal fish species. Therefore, it is reasonable to assume that population abundances will decline if the studied species cannot reproduce in freshwaters. As the Baltic Sea is a nutrient sink, it is much harder to conserve and create suitable spawning areas in the sea than in fresh water. Resource managers and conservationists should therefore assure that the rivers and creeks (together with their attached wetlands) that disembogue into the Baltic Sea are as natural as possible and managed properly. This would create and preserve suitable spawning habitats for various freshwater fishes, whilst directly and indirectly reducing nutrient levels in the sea. **Second**, it was shown that the movement patterns of the species studied are more versatile than previously thought. This new knowledge contributes to our understanding of population dynamics and species ecology, and can therefore be used in resource management and conservation actions, such as river restoration and wetland construction. **Third**, the age and growth data provided by the present thesis is of particular importance because it can be directly used to establish fishery regulations for sustainable resource management. Furthermore, such data can draw attention to the problems within populations, which allows for them to be addressed.

To conclude, present thesis utilized an innovative method to study fish in Estonian coastal waters and has significantly increased our knowledge of the biology of the species studied. The results have theoretical and applied value, and can be used in the Baltic Sea and other similar systems. The questions that remained unanswered in the present thesis should be investigated in the future.

This will most definitely include *in situ* and *ex situ* experimental work on salinity tolerance of eggs and larvae, but also elemental uptake to otoliths in different environmental settings. Future studies should make complementary use of otolith microchemistry and different tagging or/and genetic techniques, because these methods supplement each other and the most informative results are reached when they are combined.

KOKKUVÕTE

Otoliitidest saadud teadmisi Läänemeres elavate mageveekalade rännete, kudepaiga eelistuste ja vanuselise struktuuri kohta

Läänemere kalastikku kuulub nii merelisi kui ka mageveelisi liike. Paljud neist liikidest elavad füsioloogilises mõttes oma taluvuspiiril ja on tänu toitaineterikkale mereveele osa väga produktiivsest ökosüsteemist. Mageveekaladele pakub riimveeline Läänemeri paremaid toitumistingimusi, mitmekesiseid elupaiku ja osale liikidest ka kudealasid. Enamik mageveekalu sooritavad siiski anadroomseid kuderändeid magevette, mistõttu on merega ühenduses olevad jõed, järved, ojad ning kraavid neile olulised kude- ja turgutusalad. Rannikumerd asustavate mageveekalade asurkondade seisund sõltub suuresti anadroomsete kalade jõudmisest mageveelistele koelmualadele, kuid kindlasti ka koelmute kvaliteedist. Samas tuleb tõdeda, et paljudel juhtudel on nende alade kvaliteet ja ligipääsetavus inimtegevuse tagajärjel halvenenud.

Mageveesigimise osatähtsus riimvees elavate mageveekalade hulgas on seniajani suuresti teadmata. Palju ei ole teada ka nende rännete, täiendi moodustumise, vanuselise struktuuri ja kasvukiiruste kohta. Nimetatud taustandmete uurimine täiendab teadmisi mageveekalade ökoloogiast ja populatsiooni dünaamikast ning võimaldab koostada kalavarude teaduslikult põhjendatud majandamiskavasid ning toetada looduskaitselisi tegevusi.

Käesoleva doktoritöö peamiseks eesmärgiks oli uurida Läänemeres elavate mageveekalade mage- ja riimvee kasutust erinevatel elujärkudel, kasutades selleks kalade kuulmekivikestesse (otoliitidesse) nende elu jooksul salvestatud teavet. Täpsemad eesmärgid olid järgmised: 1) hinnata erinevate keemiliste markerite kasutatavust uurimisalade ja liikide kaupa (**I–III**, **V**, **VI**); 2) uurida mageveesigimise osatähtsust haugi (*Esox lucius*) (**I**, **VI**), lutsu (*Lota lota*) (**II**) ja säina (*Leuciscus idus*) (**V**) näitel; 3) uurida rändeid mage- ja riimvee vahel haugi (**I**), lutsu (**II**) ja säina (**V**) näitel; 4) määrata värvitud otoliidi ristlõigete järgi lutsu (**II**) ja säina (**IV**) vanused ning kasvukiirused. Enamik käesolevas doktoritöös kasutatud valimist koguti Väinamere regioonist. Otoliitide keemilised analüüsid teostati laserablatsiooniga varustatud induktiivselt seotud plasma mass-spektromeetriga (LA-ICPMS).

Veeproovide ja otoliitide keemilise analüüsi tulemused näitasid, et otoliidi Sr:Ca suhe võimaldab usaldusväärselt määrata kalade sigimisbiotoopi ja uurida nende liikumisi Eesti ranniku mageveekogude ja riimveelise Läänemere vahel (**I**, **II**, **V**, **VI**). Sama järeldust ei saa teha Ba:Ca suhte kohta, sest me ei suutnud tuvastada selget seost soolsusega (**II**, **V**). Käesoleva doktoritöö andmete järgi on Ba:Ca suhtel Väinameres vaid minimaalne väärtus mage- ja riimvee vaheliste rännete uurimisel. Seevastu otoliidi ^{87}Sr:^{86}Sr suhe näitas üles suurt potentsiaali haugi kudealade eristamisel (**III**). Nimetatud markerit tasub tulevikus kindlasti kasutada Läänemeres elavate, kuid magevees sigivate kalaliikide päritolu uuri-

miseks erinevatel ruumiskaaladel. Peale ^{87}Sr:^{86}Sr suhte on soovituslik paralleelselt kasutada ka teisi keemilisi markereid (nt Sr:Ca, Ba:Ca, $\delta^{18}O$, $\delta^{13}C$), eriti olukordades, kus uurimisaluseid veekogusid on väga palju või need paiknevad lähestikku.

Käesolev doktoritöö näitas, et mageveesigimine on Väinamere haugi, lutsu ja säina puhul valdav (**I**, **II**, **V**, **VI**). Uuritud liikidest oli haug sigimisbiotoobi valikul kõige plastilisem, sest 11% isenditest oli sündinud riimvees (**I**, **VI**). Üksikud lutsu ja säina Sr:Ca profiilid näitasid, et need isendid võisid olla koorunud riimvees (**II**, **V**). Tegelik mageveesigimise osakaal võib uuritud liikide seas olla ka suurem, kuna jõesuudme lähedale koetud marjaterad võivad kanduda riimvee mõjualasse (otoliiti talletub kõrgem Sr:Ca) või kui vastsed laskuvad kohe pärast koorumist merre (magevee madal Sr:Ca ei jõua otoliiti talletuda). Kirjeldatud liikumiste toimumine on ebatõenäoline, kuid väärib siiski kindlasti edaspidiseid uuringuid. Kui minevikus avaldatud töödes on välja pakutud, et Väinameres on arvukalt haugi ja säina koelmuid ning luts suudab kudeda ka riimvees, siis käesolev doktoritöö neid tulemusi ei kinnita. Samas tuleb tõdeda ka seda, et ükski varasem töö ei ole saanud kasutada otseseid analüüsiandmeid, mis kinnitaks mingi konkreetse kala sündimist magedas või riimvees – on tuginetud vaid kaudsetele andmetele.

Uuritud liikide rändestrateegiate plastilisus avaldus nii kalade esimese merre laskumise ning suguküpsuse saabumise vanuses ja suuruses kui ka üldistes rändemustrites. Enamik Matsalu lahe anadroomseid hauge laskus esmakordselt merre oma esimese kasvuhooaja jooksul, kuid vanus ja suurus varieerusid esimesel merre laskumisel rohkem, kui varasemalt Rootsi väikejõgedes näidatud (**I**). Tõenäoliselt tuleneb see uuritavate süsteemide erinevusest: Matsalu lahe delta-estuaar ja märgalad võimaldavad haugi noorjärkudel viibida magevees kauem, sest nii ruumi kui toiduküllaseid elupaiku leidub isegi veetaseme alanedes. Matsalu lahes esineva soolsuse gradiendi abil tuvastasime haugil ka mitmeid erinevaid merre liikumise mustreid ning elupaiga valikuid lahes.

Lutsu vanus ja suurus varieerusid esimesel merre laskumisel rohkem kui haugil (**II**). Enamik lutse laskus merre hilistalvel või kevadel, veel enne üheaastaseks saamist. Otoliidi Ba:Ca profiilid vihjasid, et tegemist võib olla varakevadise suurvee poolt vallandatud rändega. Tuvastati ka seni kirjeldamata rändestrateegia: varajased laskujad, kes rändasid merre esimese või teise elukuu jooksul. Enamik lutse saavutas suguküpsuse ja sooritas oma esimese anadroomse kuderände teisel või kolmandal eluaastal; samas esines ka isendeid, kes said suguküpseks 1–3 aastat hiljem. Säina merre laskumise vanus varieerus käesolevas doktoritöös uuritud kolmest liigist kõige vähem. Kui siiani teati, et säinas veedab pärast koorumist vähemalt aasta magevees, siis käesoleva doktoritöö tulemused näitasid, et Väinameres laskub säinas merre juba esimese kuu või kahe jooksul (**IV**). Järgmisel kevadel tõusevad paljud säina noorkalad uuesti magevette, tõenäoliselt koos täiskasvanud kudekaladega; seda kinnitavad ka kalameeste tähelepanekud. Kümne Matsalu lahe täiskasvanud säina puhul

tuvastasime ka selge merelise elupaiga muutuse vanuse kasvades: noorena elasid antud isendid soolasemas, kuid vanemana magedamas keskkonnas.

Lutsu ja säina vanuse ja kasvukiiruse andmed olid mitmes mõttes üllatavad. Saunja ja Matsalu lahe lutsude kasvukiirused olid vähemalt esimeste eluaastate jooksul suurimad, mis on Läänemeres ja selle valgalal eales registreeritud (**II**). Kahelt uurimisalalt pärit lutsude vanuselises koosseisus domineerisid kahe- ja kolmeaastased isendid. Hoolimata meres saavutatud suurest kasvukiirusest, on lutsu arvukus ja saagid võrreldes Peipsi järvega Väinameres madalad. Kalandusliku ja ökoloogilise kasu suurendamiseks võiks lutsule meres ja sinna suubuvate jõgede alamjooksudel kehtestada sama alammõõdu, mis Peipsis ja Võrtsjärves (täispikkus 40 cm). Säina vanuseline koosseis varieerus oluliselt Käina, Matsalu ja Saunja lahe kudekarjade vahel (**IV**). Käina lahes olid valdavad noored, keskmiselt 5–7 aasta vanused isendid. Seevastu Matsalu ja Saunja lahes olid valdavad vanad, keskmiselt 11–16aastased isendid. Kõigi kolme kudekarja määratud vanuste vahemik oli lai ja igas kudekarjas leidus üle 20 aasta vanuseid isendeid. Vanimad olid kaks 29 aasta vanust isendit Saunja lahest – teadaolevalt on need ka maailma vanimad säinad. Kudekarja vanuselise koosseisu iseärasused peegeldusid ka konkreetse kudekarja populatsiooni dünaamikas ja arvukuses: Käina lahes ning selle ümbruses on täiskasvanud ja noorkalad arvukad, kuid Matsalu ja Saunja lahes on nende arvukus väga madal. Kõik see vihjab sellele, et neis kunagistes olulistes säina kude- ja turgutusaladel esinevad suured probleemid täiendi tekkel.

Käesoleva doktoritöö tulemusi saab kasutada taustandmetena kalavarude majandamiskavade väljatöötamisel ja erinevate looduskaitseliste tegevuste toetamiseks. Esiteks oli suur osa käesolevas doktoritöös analüüsitud isenditest sündinud magevees, mistõttu on põhjust arvata, et mageveelised koelmualad omavad uuritud liikide asurkondade püsimise kontekstis suurt tähtsust. Ei saa eeldada, et käesolevas töös uuritud mageveekalad saavad parema kudemisvõimaluse puudumisel hakkama ka riimvees kudemisega. Läänemerre akumuleerub suurel hulgal toitaineid, mistõttu on meres asuvaid elupaiku palju keerulisem kaitsta ja taastada kui mageveelisi. Läänemerre suubuvate vooluveekogude looduslähedasel ja oskuslikul majandamisel tekiks erinevatele mageveekaladele hulganisti juurde kudepaiku ning väheneks toitainete kontsentratsioon meres. Teiseks näitas käesolev doktoritöö, et uurimisaluste liikide rändemustrid on keerulisemad, kui varem arvati. Kogutud andmed täiendavad meie arusaamist uuritud liikide ökoloogiast ja populatsiooni dünaamikast ning neid saab seetõttu kasutada kalavarude majandamisel ja looduskaitselistes tegevustes (nt jõgede taastamine või märgalade loomine). Kolmandaks saab vanuse ja kasvukiiruse andmeid otseselt kasutada jätkusuutliku kalavaru majandamise tagamiseks. Samuti võivad need teadmised juhtida tähelepanu probleemidele populatsioonide või kudekarjade sees, mida saab siis hiljem juba täpsemalt uurida.

Käesolev doktoritöö kasutas (Eesti kontekstis) uudset meetodit erinevate ihtüoloogiliste küsimuste uurimiseks ja suurendas teadmisi uurimisaluste liikide bioloogiast. Kogutud teadmisi saab kasutada Läänemeres või sarnastes süsteemides. Käesolevas töös vastamata jäänud küsimused vajaksid tulevikus kindlasti katselisi uuringuid. Edaspidiste uuringute raames tuleks kaaluda ka otoliidi mikrokeemia ühildamist erinevate märgistamise või/ja geneetiliste meetoditega, sest nimetatud meetodid täiendavad üksteist ja on kõige tulemuslikumad omavahel seotuna.

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PUBLICATIONS

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Rohtla, M., Vetemaa, M., Urtson, K. & Soesoo, A. 2012. Early life migration patterns of Baltic Sea pike *Esox lucius*. *Journal of Fish Biology* 80, 886–893.

Verliin, A., Saks, L., Svirgsden, R., Vetemaa, M., Rohtla, M., Taal, I. & Saat, T. 2013. Whitefish (*Coregonus lavaretus* (L.)) landings in the Baltic Sea during the past 100 years: combining official datasets and grey literature. *Advances in Limnology* 64, 133–152.

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Conference presentations:

Rohtla, M., Urtson, K. & Vetemaa, M. Using the microchemical constituent of otoliths to study fish migrations (oral presentation). Next generation insights into geosciences and ecology. Tartu, Estonia, 12–13 May, 2011.

Rohtla, M., Vetemaa, M., Taal, I. & Saat, T. Migrations of anadromous burbot (*Lota lota*) in the brackish Baltic Sea. Ecology and Conservation of Freshwater Fish (poster presentation). Vila Nova de Cerveira, Portugal, 28 May – 2 June, 2012.

Rohtla, M. Otoliitide mikrokeemia kasutamine kalade rännete uuringutes (oral presentation) Zooloogia konverents. Tartu, Estonia, 5th April, 2013.

Rohtla, M., Svirgsden, R., Verliin, A., Rumvolt, K., Matetski, L. & Vetemaa, M. Provenance and migration patterns of European whitefish *Coregonus lavaretus* (L.) s.l. in the Baltic Sea – combining otolith geochemistry and gill raker counts (oral presentation). 5th International Otolith Symposium. Mallorca, Spain, 20–24 October 2014.

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Rohtla, M., Vetemaa, M., Urtson, K. & Soesoo, A. 2012. Early life migration patterns of Baltic Sea pike *Esox lucius*. *Journal of Fish Biology* 80, 886–893.

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Konverentsiettekanded:

Rohtla, M., Urtson, K. & Vetemaa, M. Using the microchemical constituent of otoliths to study fish migrations (suuline ettekanne). Next generation insights into geosciences and ecology. Tartu, Eesti, 12–13.05.2011.

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